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Predation on Bivalve Veligers by Polychaete Larvae

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Abstract. Polychaete larvae from several families are thought to be natural predators upon planktonic bivalve larvae. However, little direct evidence of interactions between these predators and prey is available. We conducted predator-prey experiments on laboratory roller tables for five putative predatory polychaete larvae, representing four families (metatroch-less larvae of the Polynoidae and metatrochophore larvae of the Spionidae, the Magelonidae, and the Phyllodocidae). D-hinge veliger larvae of the oyster *Crassostrea gigas* were offered as prey. Predation was monitored over a range of prey densities and in the presence and absence of background plankton. "Background plankton" are any naturally occurring plankton assemblages found in whole, unfiltered seawater at ambient concentrations. For all polychaete larvae examined, when natural *C. gigas* densities *and* background plankton were used, no predation was observed. Magelonids and phyllodocids did not consume any *C. gigas* larvae, regardless of conditions. Polynoid and spionid trochophores consumed *C. gigas* veligers at both the "natural" and unnaturally high prey densities in filtered seawater. The addition of background plankton eliminated the predation at all natural prey densities and significantly reduced the predation observed at high prey densities.

Introduction

Predation in the plankton is a source of mortality that may control the presence and abundance of the planktonic larvae of benthic marine invertebrates (Thorson, 1950). Observations of predation upon meroplanktonic invertebrate larvae are recorded from as far back as the 1920s. For example, Lebour (1922) noted bivalve veliger larvae in the guts of the larval polychaete *Magelona papillicornis* (Magelonidae). Other biologists have also observed bivalve veligers within the guts of field-caught *Magelona* sp. larvae (Thorson, 1946; Smidt, 1951; Kühl, 1974; Wilson, 1982). Lebour (1922), Smidt (1951), and Kühl (1974) recorded only bivalve larvae as prey for magelonids, but Thorson (1946) and Wilson (1982) observed that *M. papillicornis* also consumed other planktonic organisms. In spite of these many observations and the general impression that larval polychaetes of the genus *Magelona* are specialist predators of bivalve veligers (*e.g.*, Todd *et al.*, 1996), a natural predator-prey relationship between larval polychaetes and bivalve larvae has yet to be definitively shown. There are problems also with the anecdotal nature of some past observations on wild-caught plankton: when planktonic predators and prey are concentrated in the cod-end of a plankton net for several minutes or more, as is usually the case when plankton samples are being collected, it is not possible to differentiate natural predation from that occurring in the cod-end under very abnormal conditions, which we refer to as "artifactual predation."

Predation upon bivalve veligers by polychaete trochophores (metatroch-less trochophores and metatrochophores) has also been observed for representatives of other polychaete families, including the Polynoidae (Yokouchi, 1991), the Nephtyidae (Mileikovski, 1959; Yokouchi, 1991), the Phyllodocidae (Yokouchi, 1991), and the Spionidae (Daro and Polk, 1973; K. B. Johnson, unpubl. data). These observations of predation are remarkable in two ways. First, it is very seldom that a larva has been observed to be the primary food consumed by a planktonic suspension-feeding predator that consumes its prey one individual at a time. Unlike cases in which predators (*e.g.*, some scyphozoans and clupeid fish) indiscriminately feed on many planktonic prey, consistent observations of a given prey item in the gut of such a "single-

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particle predator" may indicate a strongly specific predator-prey relationship and provide insight into predator behavior. Second, bivalve veligers consumed by polychaete larvae are often surprisingly large relative to the predator's body diameter and apparent mouth size (see Fig. 1).

Examining the mechanism underlying particle ingestion by polychaete larvae, Phillips and Pernet (1996) fed larvae of the polychaetes *Serpula vermicularis* (Serpulidae) and *Arctonöe vittata* (Polynoidae) polystyrene beads and plankton at a range of sizes. *S. vermicularis* larvae were apparently not equipped to handle food particles greater than 12 μm in diameter (Phillips and Pernet, 1996). *A. vittata* larvae less than 100 μm in diameter were observed to ingest large particles (polystyrene beads and phytoplankton) up to 60 μm in diameter, a common size for small bivalve larvae. The larvae of *A. vittata*, a scaleworm, likely include relatively large particles in their natural diet. Does this diet include larval bivalves? Bivalve veligers have been observed in the guts of field-caught polynoid larvae (Yokouchi, 1991). Like the larvae of *Magelona* sp., the larvae of polynoids and several other polychaete families may be natural predators upon bivalve veligers.

We examined the potential predator-prey relationship between several larval polychaetes and bivalve veliger larvae. The relationship was examined using a combination of field observations (plankton samples) and laboratory experiments. In plankton samples, trochophores representing several families were observed with bivalve veligers in their guts. More important for this study, however, field samples helped determine densities used in laboratory experiments. Densities of predators and prey reflected field densities from samples in which predation was observed. Laboratory experiments used five types of larval polychaetes as predators: *A. vittata* (metatroch-less trochophore, Polynoidae), *Magelona* sp. (metatrochophore, Magelonidae), and unidentified species from the families Polynoidae (metatroch-less trochophore), Spionidae (metatrochophore), and Phyllodocidae (metatrochophore). D-hinge veliger larvae of the oyster *Crassostrea gigas* were offered as prey. Experiments were conducted at two prey densities and in the presence or absence of background plankton. The presence of background plankton (by which we mean naturally occurring phyto- and zooplankton ever-present in the field but often excluded in laboratory experiments) is potentially important because it may act as a substitute food for predators or obscure prey from detection (Johnson and Shanks, 1997).

Materials and Methods

Field observations

During August 1994, plankton samples were collected from within 10 km of the shore of Duck, North Carolina. Using a 100-μm-mesh plankton net and an on-board electric centrifugal pump, samples were collected for 3 min at 227.1 l min^{-1}, for a final sample volume of approximately 680 liters. Between 3 and 5 sampling depths were chosen at each station, depending upon the station depth. After pumping was complete, samples were rinsed from the cod-ends and preserved with 10% $CaCO_3$-buffered formalin for later sorting. Plankton samples were sorted under a dissection microscope with polarized light to aid in locating bivalves. For a more detailed description of collection and sorting methods, see Brink (1997).

Bivalve veligers were tallied when observed in the guts of predatory polychaete larvae. The total density of bivalve larvae and polychaete larvae was determined for each sample in which bivalve predation was observed. These densities were considered when deciding upon predator and prey densities to be used in the laboratory experiments described below.

Culture of predators and prey

Adult specimens of the scaleworm *Arctonöe vittata*, commensal with the keyhole limpet *Diodora aspera*, were collected with their host from the west shore rocky intertidal of San Juan Island, Washington. Individuals of *A. vittata* were spawned and larvae were cultured using the methods described by Phillips and Pernet (1996) with the addition of *Coscinodiscus radiatus* (CCMP 310) as a food source. Fertilized eggs were cultured in 600-ml beakers at densities of ~500 l^{-1}. Larvae approximately 21 days old were used as predators in experiments.

All other larval polychaetes used as predators were collected at high tide near the mouth of Coos Bay, Oregon, by slowly towing a 150-μm-mesh plankton net equipped with a large, blind cod-end (Reeve, 1981). Pipettes (3-mm-bore) were used to immediately remove predators from the plankton sample and isolate them in 250 ml of filtered seawater. Experiments began within 6 hours of predator collection.

D-hinge veligers of the oyster *Crassostrea gigas*, 5 to 10 days old (greatest linear dimension 70–90 μm), were used as prey in all laboratory experiments. The oyster larvae were obtained from Whiskey Creek Oyster Farms, Tillamook, Oregon, and maintained in 1-gallon jars on a diet of *Isochrysis galbana* and *Rhodomonas* sp.

Roller table experiments

One laboratory experiment, with four treatments, was conducted for each of the five species of larval polychaete (Table I). Two densities of prey were used. The first prey density (Treatments A and B) was designed to approximate natural field concentrations and was set at 33 bivalve larvae l^{-1} on the basis of the highest value we found in the literature (Carriker, 1951). The second prey density

Table I

Mean number of Crassostrea gigas *veliger larvae in individual guts of predatory larval polychaetes according to treatment (prey density and the presence or absence of background plankton) ± the 95% confidence interval*

	Treatment			
	Near-natural prey density (33 prey l^{-1})		High prey density (1000 prey l^{-1})	
Larval polychaete (body length in parentheses)	Filtered seawater A	Background plankton **B**	Filtered seawater C	Background plankton D
Magelona sp. (2–3 mm)	0	**0**	0	0
Phyllodocid A (300–360 μm)	0	**0**	0	0
A. vittata (260–290 μm)	1.05 ± 0.37	**0**	4.17 ± 0.64	0.72 ± 0.38
Polynoid A (280–310 μm)	0.83 ± 0.41	**0**	6.17 ± 0.79	1.33 ± 0.44
Spionid A (400–500 μm)	0.08 ± 0.16	**0**	1.33 ± 0.37	0.50 ± 0.38

Results of Treatment B, the most natural treatment in regard to prey density and the presence of background plankton, are in bold.

(Treatments C and D) was chosen to represent an unnaturally high concentration (1000 l^{-1}) and thus increase the likelihood that the prey would be encountered and ingested by predators. Each prey density was presented to predators in either filtered seawater (Treatments A and C) or with background plankton (Treatments B and D). Background plankton was collected by filling buckets with whole, unfiltered seawater at the high tide immediately preceding the start of an experiment. To fill background treatment tanks, the seawater in buckets was stirred gently, suspending settled plankton, and then poured into tanks.

For each experiment, all treatments and replicates were conducted simultaneously. Cylindrical 3-l tanks (19 cm dia. × 10.5 cm ht.) were placed on a roller table (Omori and Ikeda, 1984; Larson and Shanks, 1996) maintained at 12°C in a constant temperature room with a 14:10 light:dark cycle. The slow (1 rpm) rotation of the tanks kept the plankton from settling, and the experiments were of short duration (24 h) to prevent oxygen depletion (Larson and Shanks, 1996). At the close of the experiments, the water in the roller table tanks was filtered through a partially submerged 20-μm-mesh Nitex filter, and each tank was rinsed twice to ensure that all polychaete larvae were retrieved. Within 2.5 min of filtration, polychaetes were located and isolated in filtered seawater. Consumed bivalve larvae, visible through the polychaete larva's transparent body, were then counted.

The experiment using *Arctonöe vittata* larvae as predators was conducted at Friday Harbor Laboratories (Friday Harbor, Washington). A predator density of 2 l^{-1} (6 predators per tank) was chosen based upon the upper range of polychaete trochophore densities from our field samples in which predation upon bivalve larvae had been observed. Each tank was replicated three times. Thus, a total of 18 polychaete larvae were used as predators for each treatment.

All other experiments were conducted at the Oregon Institute of Marine Biology (Coos Bay, Oregon). The four species of larval polychaetes used as predators were *Magelona* sp. (metatrochophores) and three unidentified species representing the families Polynoidae (metatroch-less trochophores), Spionidae (metatrochophores), and Phyllodocidae (metatrochophores). The unidentified genera will be referred to as polynoid A, spionid A, and phyllodocid A, respectively. All predator densities in Coos Bay experiments were 1 l^{-1} (3 predators per tank) and, for each treatment, tanks were replicated four times.

Results

Field observations

Of 150 samples, 18 had at least one polychaete larva that had preyed upon a bivalve veliger. A total of 30 bivalves were observed in the guts of 25 polychaete larvae (20 trochophores and 5 metatrochophores). The number of bivalves consumed by each of the 20 metatroch-less trochophores was variable: 1 trochophore larva had 3 bivalves, 2 trochophore larvae had 2 bivalves each, and 17 trochophore larvae had 1 bivalve each. Trochophores were typically large (mean body length = 237 μm, SD = 35 μm) and robust in form (for examples of body shape, see illustrations of polynoids, phyllodocids, or nephtyids in Bhaud and Cazaux, 1987). Detailed identification of

these metatroch-less trochophores was often not possible, but the following families may have been represented: Phyllodocidae, Hesionidae, early Nephtyidae, Polynoidae, and Chrysopetalidae. Of those metatrochophores that had bivalves, 3 were *Magelona* sp. with 1 bivalve each. The last 2 metatrochophores were likely either phyllodocids or hesionids; one (380 μm in length) had 2 bivalves in its gut, while the other (368 μm in length) had 1 bivalve. In addition, a single metatroch-less polychaete larva was observed with a gastropod veliger in its gut.

For the 18 samples in which bivalves were observed in polychaete larva guts, densities ranged from 42 to 1193 polychaete larvae sample^{-1} ($\bar{x}$ = 277.2, SD = 324.3). The range of larval bivalve densities in these same samples was from 419 to 1949 larvae sample^{-1} ($\bar{x}$ = 1217.6, SD = 494.2). Therefore, at least 42 trochophores and 419 bivalve larvae were concentrated together in the cod-end bucket (about 200 ml of seawater) when a sample was complete.

Roller table experiments

Table I summarizes the results of the roller table experiments. For the larvae of *Magelona* sp. and phyllodocid A, predation on bivalve veligers was not observed in the laboratory under any conditions. The larvae of *Arctonöe vittata*, polynoid A, and spionid A, however, did consume *Crassostrea gigas* veligers (Fig. 1). These three polychaetes exhibited low levels of predation when veliger larvae were presented at near-natural densities and in filtered seawater (Table I, Treatment A). When background plankton was used with this same near-natural prey density, predation was always absent (Table I, Treatment B). Predation was most frequent when densities of *C. gigas* were high in filtered seawater (Table I, Treatment C). Notably, the polynoid larvae, *A. vittata* and polynoid A, consumed the greatest numbers of veligers in Treatment C. The most extreme was polynoid A, averaging 6.17 bivalve veligers gut^{-1} with two of the individuals consuming 8 veligers each. Presenting prey at high densities in the presence of background plankton (Table I, Treatment D) reduced, but did not eliminate, the predation observed at the same densities in Treatment C.

Polynoid trochophores, which consumed numerous veligers in Treatment C, voided their gut contents through a large posterior rupture. This rupture quickly heals and the unburdened trochophore suffers no obvious permanent damage. Veliger valves sometimes remain attached at the hinge after passage through the gut. Intact veligers that passed through the guts of larval polychaetes were isolated in filtered seawater, but no consumed veligers revived. Thus, although digestion by trochophores can be incomplete, predation does appear to result in mortality for bivalve larvae.

Discussion

None of the larval polychaete species we tested consumed any bivalve larvae when laboratory conditions were the closest to natural (*i.e.*, near-natural prey density with background plankton present; Table I, Treatment B). We did observe predation in the treatments that used unnatural prey density or filtered seawater. One explanation for the lack of predation in Treatment B could be that larval polychaetes are not natural predators of bivalve veliger larvae. In that case, previously published observations of bivalve veligers in the guts of larval polychaetes might be an artifact of the concentration of predators and prey in cod-end buckets during plankton tows. Such artificial conditions can alter the behavior of predators and prey and increase the probability of encounters between them, resulting in unnatural ingestion. Cod-end predation is well documented for other planktonic predators, such as chaetognaths (Feigenbaum and Maris, 1984), and may mislead observers about predator-prey relationships.

Low encounter rates might also explain the absence of predation under the most natural laboratory conditions used in this study. Predators and prey may simply not encounter one another during the experiment. Natural prey densities, which tend to be relatively low, and the presence of background plankton can both decrease the number of encounters between predators and prey (Johnson and Shanks, 1997). For example, lack of encounters may explain the low predation by *Arctonöe vittata* on *Crassostrea gigas* under the most natural conditions (Table I, Treatment B). This explanation is supported by comparisons between observed predation by *A. vittata* and encounter model estimates (K. B. Johnson, unpubl. data): the estimates produced by two models (Gerritsen and Strickler, 1977, and a simple clearance rate model) were statistically indistinguishable from the minimum known encounters of *A. vittata* with *C. gigas* (*i.e.*, observed predation events). This bolsters the argument that larval polychaetes naturally prey upon bivalve veligers during relatively infrequent encounters. Indeed, the many published observations of predation (*e.g.*, Thorson, 1946; Smidt, 1951; Kühl, 1974; Wilson, 1982) may reflect relatively rare field encounters rather than artifactual cod-end predation. Predator-prey encounters in these previously published studies can, however, be difficult to estimate. Field densities, swimming speeds, and encounter radiuses, essential components of encounter rate models, are often unknown. Finally, the hypothesis that these polychaetes may, upon infrequent encounters, be natural predators of bivalve larvae is also supported by an observation of a spionid larva with one *C. gigas* veliger in its gut (K. B. Johnson, unpubl. data). This metatrochophore larva was fixed only seconds after being collected in a 120-l sample

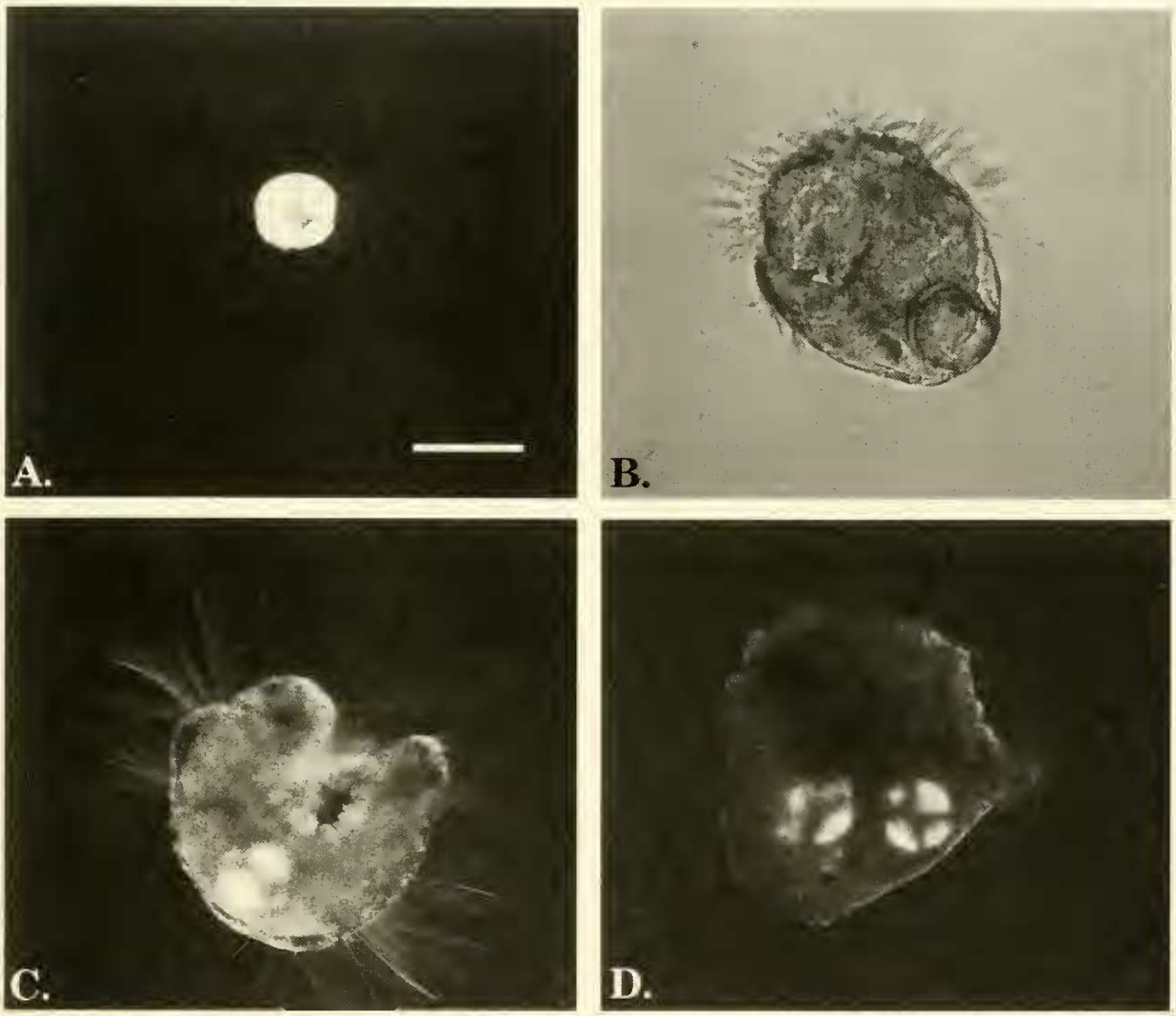

Figure 1. (A) D-hinge veliger of the oyster *Crassostrea gigas*. (B) Trochophore larva of the polynoid *Arctonöe vittata* with a veliger of the oyster *C. gigas* in its gut. (C) Metatrochophore larva of spionid A with a *C. gigas* veliger in its gut. (D) Trochophore larva of polynoid A with two *C. gigas* veligers in its gut. A, C, and D are viewed with cross-polarized light. Scale bar = 100 μm.

of seawater. No plankton net was towed; the water was collected in a plastic bag, then immediately concentrated and fixed. This method allowed little time for artifactual predation.

The true frequency of encounters between predators and prey in the field may, however, be far greater than estimated by models or from laboratory experiments if natural densities are greater than those recorded by investigators. The effect of plankton patchiness on sampling accuracy has received some attention (Hamner and Carleton, 1979; Omori and Hamner, 1982) and could cause underestimation of field densities. Plankton can be highly concentrated in a localized area—for example, through behavior-related aggregation (*e.g.*, Alldredge and Hamner, 1980; Ueda *et al.*, 1983) or the accumulation of plankton in a front (Stommel, 1949; Bray, 1953; George and Edwards, 1973). A net towed through such a patch and then through a sparsely populated region would collect a sample with an apparent density lower than the actual density within the front or aggregation. Furthermore, bivalve veligers are known to associate with marine snow (Green and Dagg, 1997; Shanks and Walters, 1997), creating localized high larval densities. Larval polychaetes can also be strongly associated with marine snow (Shanks and del Carmen, 1997) and, as a result, may encounter potential prey items such as bivalve veligers more frequently. Published observations of predation upon bivalve veligers by larval polychaetes may thus re-

flect natural predation in concentrated patches of predators and prey.

In spite of the fact that we never observed predation on bivalve veligers by *Magelona* larvae in laboratory experiments, published observations of this predator-prey relationship are numerous and should not be summarily dismissed. Wilson (1982) mentions that three species of *Magelona* are known to be carnivorous in later stages and includes descriptions of late-stage metatrochophore larvae > 4 mm in length. The *Magelona* metatrochophore larvae used in our experiments were 2—3 mm long. At a later stage, with larger palps and mouths, these larvae may be more effective at capturing bivalve larvae. It should be noted, however, that a larva of *Magelona papillicornis*, lacking long palps and only 1 mm in length, is depicted by Todd *et al.* (1996) with a bivalve veliger in its gut. Experiments analogous to ours should be conducted with later stage *Magelona* larvae to clarify the relationship of this predator with potential bivalve prey.

Summary

Certain larval polychaetes may be significant natural predators upon bivalve veligers. This investigation, however, provides laboratory evidence that natural predation on bivalve larvae by polychaete larvae is absent or uncommon, possibly because the predators and prey have few encounters in the field (assuming that published larval bivalve densities accurately reflect natural densities).

Published reports of bivalve veligers in the guts of larval polychaetes suggest a natural predator-prey relationship and are seemingly incongruous with our results. One possible explanation is that polychaete larvae consumed the veligers while in the cod-end of a plankton net, making the predation an artifact of the collection method.

When polychaete larvae consumed bivalve veligers in our laboratory experiments, the use of near-natural prey densities with natural background plankton completely eliminated predation. This lack of predation may be due to a reduction in the number of encounters with prey (published data indicates that natural densities of bivalve larvae are relatively low) or to the role of background plankton as a substitute food for predators or a screen to obscure prey from detection. In short, our results suggest that a natural predator-prey relationship between polychaete larvae and bivalve veligers may not exist. If a relationship does exist, then the frequency of interaction and its ecological importance may be less than expected on the basis of published observations.

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